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Temporal and spatial succession and dynamics of soil fungal communities in restored grassland on the Loess Plateau in China

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Abstract

Natural secondary succession of degraded soil has improved the ecological environment of the Loess Plateau, profoundly influencing the succession and dynamics of soil fungal communities restored grasslands in particular. This chronosequence and the varied topography of the Loess Plateau thus provide a unique opportunity to synchronously investigate the variation of soil quality and fungal communities as they develop over time and space. Here, we used high-throughput sequencing of the ITS rRNA gene region to analyze the fungal community at a local scale. Edaphic variables and fungal community characteristics were compared among three restoration durations (5, 20, and 30 years), two soil layers (topsoil and subsoil), and different topographic factors (slope positions and aspects). Edaphic variables displayed varying patterns with significant differences among restoration durations and soil layers, but no such topographic patterns were found. As succession proceeded, alpha and beta diversities of fungal communities changed as space changed; whereas, over time, the discrepancy in community composition between the two soil layers declined. Constructed co-occurrence networks of edaphic variables combined with fungal community composition and distribution patterns based on indicator and keystone species also varied among three durations. Fungal trophic guilds showed a contrasting distribution between the two soil layers, but they closely followed the soil nutrient conditions and metabolic characteristics of keystone species. Our results demonstrated that predictable spatial variation occurs in soil fungal communities in tandem with temporal succession and dynamics of indicator and keystone species in restored grassland on the Loess Plateau.

KEYWORDS

co-occurrence network, fungal community, loess plateau, soil quality, succession

1 | INTRODUCTION

The Loess Plateau has suffered serious ecological degradation, particularly severe water and soil erosion of its soil (Nearing, Xie, Liu, & Ye, 2017). This pressing issue is largely because of growing population pressure and environmental damage not checked by reasonable and responsible land management (Fu et al., 2016). In 1998, the Chinese government initiated the well-known 'Grain-to-Green' Program on the Loess Plateau (Deng, Liu, & Shangguan, 2015; Feng et al., 2016). Much research has focused on ecological recovery by replanting

native vegetation (Yang, Dou, & An, 2017) or soil quality assessments in this unique region (Dang et al., 2017; Zhang, 2017). Through vegetation restoration of the Loess Plateau, its croplands were converted into grasslands or shrubs via natural succession. Both soil conditions and vegetation coverage have been improved, along with soil microbial community succession fostered by greater ecological stability in restored lands compared with degraded lands on the Loess Plateau (Guo et al., 2018; Liu et al., 2017; Zhang, Liu, Xue, & Wang, 2016).

In this context, distribution patterns of the soil microbial community and their drivers are central issues, as they are crucial for understanding and predicting the role played by soil microbes in maintaining ecosystem functioning and stability when making land management decisions (Kubartová, Ottosson, Dahlberg, & Stenlid, 2012). An enhanced appreciation of the link between environment and microbial ecology, in recent years, has led to many studies focused on soil bacterial communities in the Loess Plateau region (Dang et al., 2017; Xue, Ren, Li, Leng, & Yao, 2017). The crucial contribution of soil fungi for determining the decomposition of recalcitrant carbon (Treseder, Marusenko, Romero-Olivares, & Maltz, 2016) and nutrient cycling in terrestrial ecosystems (Tedersoo et al., 2014) is now established. Although less well studied is the succession of soil fungal communities along a long-term restoration chronosequence combined with their spatial discrepancy. From ecosystems in transition, such as this chronosequence of restored grasslands, we can extract valuable information on microbial community shifts and consequently how these may contribute to soil ecosystem development. To sum it up: it would be timely to evaluate the ecological restoration process and status from the perspective of soil fungal community succession combined with soil quality analysis across time and space.

Fungi harbor a large proportion of Earth's genetic diversity and fungal activity influences the structure of plant and animal communities as well as rates of ecosystem processes (Peay, Kennedy, & Talbot, 2016). Undoubtedly, the distributions and dynamics of soil fungal communities have been extensively studied. For example, at the local scale (within 28 km distance), soil fungal communities were found distributed along an age gradient of managed *Pinus sylvestris* stands (Kyaschenko, Clemmensen, Hagenbo, Karltun, & Lindahl, 2017) and to reciprocally interact with plant factors and soil properties (Bender et al., 2014; Heijden, Bruin, Luckerhoff, Logtestijn, & Schlaeppi, 2016). Along with elevation gradient, soil fungal communities show lineage-specific biogeographic patterns in grassland system (Pellissier et al., 2014); similarly, abiotic factors and woody sagebrush range expansion have significant effects on the patterns that soil fungal diversity declines and community composition changes with increasing elevation in shrubland system (Collins, Stajich, Weber, Pombubpa, & Diez, 2018). In addition, soil fungal species composition differs between forests, depending on the dominant tree species (Yamashita & Hijii, 2006) and forest management practices (Kranabetter, Friesen, Gamiet, & Kroeger, 2005). On the Loess Plateau, one study reported that land use types can affect soil fungal community composition (Yang, Dou, Huang, & An, 2017). In stark contrast, soil fungal communities generally remain poorly studied in restored lands compared with soil bacterial communities (Anderson & Cairney, 2004; Pautasso, 2013; Tedersoo et al., 2014).

Soil bacteria and fungi can have different biogeographic patterns and environmental filters as well as co-occurrence patterns over continental scales, implying their distinctive community assembly mechanisms and ecological functions (Ma et al., 2017; Xiao, Liang, Zhou, Zhuang, & Sun, 2018). The co-occurrence networks of soil fungal and bacterial communities are varied in different spatial habitats and keystone species in networks changed with alterations in soil nutrient levels (Zheng, Zhao, Gong, Zhai, & Li, 2018). Fungi and bacteria prefer to decompose recalcitrant soil carbon and simple carbohydrates, respectively (Xiao et al., 2018). They are often presumed to be more important in natural ecosystems than in intensively managed systems that are mostly dominated by bacteria (Franciska T. de Vries, Hoffland, Nvan, Brussaard, & Bloem, 2006). The communities of soil bacteria and fungi are correlated with different soil edaphic factors under two distinct grazing systems dominating on the Tibetan Plateau (Yang et al., 2019). In particular, strong interactions occur between soil fungal diversity and edaphic variables in natural ecosystems (Zhang, Dong, et al., 2017), and soil fungi may be greater affected by the process of woody plant encroachment compared with soil bacteria (Hollister, Schadt, Palumbo, James Ansley, & Boutton, 2010). The restoration of grasslands changes the local environment, by directly modifying the litter layer, root systems, and their exudates as well indirectly affecting edaphic variables that eventually translate into alterations in ecological succession (Franciska T. de Vries et al., 2006). Only by exploring fungal distribution patterns and dynamics could we obtain a comprehensive recognition how they develop across time and space in a restored ecosystem environment. Yet, such knowledge, especially of environmental adaptation of soil fungal communities, is rarely elucidated because many soil fungal species remain unrecognized and feature complicated interactions with edaphic factors. Some of the main obstacles to the study of fungal dynamics are the heterogeneity of growth environments and the limited scope of laboratory experiments. There is one study that presents a highly versatile tool combining image analysis and graph theory to monitor spatio-temporal fungal dynamics (Vidal-Diez de Ulzurrun et al., 2015). Using traditional tissue isolation method, community structure and temporal dynamics of fungi from bagged fruits and unbagged fruits were investigated in apple orchards (Xue et al., 2016). And that due to the cost reduction and efficiency improvement of next-generation sequencing, which was used to explore the soil fungal dynamics at the community level as an effective means (Chen et al., 2017).

Currently, the response of soil fungal communities to vegetation succession is an outstanding problem in microbial ecology, one tackled by much complex research (Gao et al., 2018; Hannula et al., 2017; Purahong, Wubet, Kruger, & Buscot, 2017; Tedersoo et al., 2014). Succession in a particular environment assumes, by definition, that communities change over time in an orderly manner (Koch, Brown, & Lomolino, 1998). A soil chronosequence is a powerful tool for studying the rates and directions of soil development (Huggett, 1998). Not surprisingly, due to this unique characteristic, it has been widely used to study changing patterns and drivers of soil fungal communities over

long time scales (i.e., succession) under natural conditions (Clemmensen et al., 2015; Dang et al., 2017). By extension, we could view different timeframes of restoration (i.e., years of restoration) in terms of temporal development during the conversion of ex-arable land to grassland. Meanwhile, spatial variation in soil fungal communities also has been demonstrated by copious amounts of data collected with respect to large distances (Zhang, Adams, et al., 2017), soil profiles (Toju, Kishida, Katayama, & Takagi, 2016), and topographic variability that creates diverse microhabitat heterogeneity (Ana & Joséj, 2010).

Topography is seen as a chief factor for ecological specialization (Harms, Condit, Hubbell, & Foster, 2001), in that it must greatly affect abiotic environmental factors associated with the spatial distribution of soil fungal communities (Trudell & Edmonds, 2004). We also know that the spatial distribution patterns of soil fungi can differ within a forest setting, over a small spatial scale, because of its heterogeneous environment (Yamashita & Hijii, 2006). Knowledge of succession patterns of soil fungal communities is deemed essential to fully understand the process of soil erosion and it may also help with developing strategies to restore degraded soil ecosystems (Zhang, 2017). Nevertheless, synchronous information on the temporal and spatial distribution patterns and dynamics of soil fungal communities is rather limited, particularly at a local small scale.

Here, to solve this problem, we used high-throughput pyrosequencing (Illumina) of the internal transcribed spacer (ITS) sequence to investigate the temporal and spatial successional patterns of soil fungal communities coupled to edaphic variables and their co-occurrence networks in a conservation region of the Loess Plateau. The objectives of the present study were (i) to elucidate general temporal and spatial variation in soil quality, (b) to illustrate spatial patterns of fungal alpha and beta diversities over time during succession, and (c) to determine the co-occurrence networks and dynamics of fungal communities in terms of their functional adaptation to a changing soil environment.

2 | METHODS AND MATERIALS

2.1 | Study site

A field experiment was carried out in a restored grassland, part of a long-term natural ecological restoration region that has recovered from ex-arable land. This study area is located at the Yunwu Mountains (106°21′–106°27′ E, 36°10′–36°17′ N), in the southern part of the Ningxia Hui Autonomous Region (~45 km from the city) in Northeast China. At an altitude of 1800–2070 m in the Loess Plateau hinterland, this area supports a typical grassland vegetation type, and our field site is in a semiarid climate zone, characterized by a typical continental and monsoon climate. Its average annual temperature and annual accumulated temperature are 7°C and 2847–3592°C, respectively. Average annual sunshine duration is 2300–2500 hr and average annual precipitation is 425 mm, with 60%–75% of summer precipitation coming between July and September. The protected areas here include 297 known wild plant species, of which *Stipa bungeana*, *Stipa grandis*, *Thymus mongolicus*, *Artemisia sacrorum*, and *Potentilla acaulis* are currently the most abundant; a dominant single species is lacking because existing temporal and spatial divergence. The soil is derived from wind-blown deposits and classified as loessial (Calcaric Cambisol according to Food and Agriculture Organization (FAO) classification). This study area used as an experimental field was initiated by the Institute of Soil and Water Conservation (Yangling, Shaanxi Province, China) to monitor vegetation restoration.

2.2 | Soil sampling

We chose three restoration durations (i.e., 5, 20, and 30 years) based on their well-dated successional chronosequence. From each, we collected soil samples from different slope positions (down- and up-slope) and aspects (shaded- and sunny-slope locations) at two soil depths in July 2016. The three restoration sites had similar slope gradients (21°–25°), elevations (1890–2050 m), and prior agricultural practices (millet [*Setaria italica*] and soybean [*Glycine max*] crops grown in rotation). At each slope position, six 20-cm × 20-cm plots were established (Figure S1). All 144 sampling plots—three restoration durations × two soil layers × two slope positions × two slope aspects × six replicates (with 15 m interval)—were free of lichens, biological crusts, and any other vegetation within a radius of 0.75 m. After removing the litter horizon, soil samples were taken from the topsoil (0–20 cm) and subsoil (20–40 cm) in each plot using a stainless-steel corer (5-cm diameter). From each plot, five soil cores were collected following a Z-shaped pattern and mixed to form a single plot-level composite sample. All samples were then placed into two groups of sterile plastic bags and taken to the laboratory. One group was immediately transported on ice and stored at −80°C for the DNA analysis, whereas the other was kept at normal room temperatures before being air-dried and sieved through a 0.25-mm nylon mesh for the soil quality analysis.

2.3 | Soil physico-chemical characteristics analysis

Edaphic variables were determined using standard procedures (Bao, 2005) in duplicate, with samples randomized before any analysis to avoid batch effects. Briefly, soil pH was determined in a 1:2.5 (soil: water, *w*/*v*) soil suspension in distilled water. Soil water content (SWC) was obtained by weighing the soil and calculating the mass lost after oven-drying at 105°C to a stable weight (ca. 24 hr). Soil organic matter (SOM) content was determined by the Walkley–Black method (De Vos, Lettens, Muys, & Deckers, 2010) and total nitrogen (TN) quantified following the Kjeldahl method (Purcell & King, 1996). Total P (TP) and available P (AP) were extracted using sodium bicarbonate and measured by the molybdenum blue method (Christie, Murphy, Stevens, & Christie, 2005) on a Skalar Santt auto-analyzer (SanPlus System, Breda, Netherlands); both NO_3^- -N and NH_4^+-N were quantified by extraction with 2 M of KCl, steam distillation, and titration (Stark & Hart, 1996). Available potassium (AK), cation

exchange capacity (CEC), and calcium carbonate ($CaCO_3$) were measured using routine methods (Bao, 2005). Stoichiometry was used to examine the balance of elements relative to each other (e.g., C/N ratio; Hu et al., 2016).

2.4 | DNA extraction, high-throughput pyrosequencing, and data processing

Using 0.5 g subsample of soil, total DNA was extracted with the Fast DNA®SPIN Kit (MP Biochemicals, Solon, Ohio) following the manufacturer's procedure. To obtain sufficient DNA quantity for sequencing and to ensure an adequate soil representation, five replicates were used and pooled per sample. DNA was then quantified using a Nanodrop 1000 spectrophotometer (Thermo Scientific, Wilmington, Germany) and stored at −20°C until the next experiment. The broad-spectrum fungal primers ITS5-1737F (GGAAGTAAAAGTCGTAACAAGG) and ITS2-2043R (GCTGCGTTCTTCATCGATGC) were used to amplify the ITS1 region (Hao, Song, Mu, Hu, & Xiao, 2016). The polymerase chain reaction amplifications were made in triplicate for each sample, and the amplicon samples sequenced on a paired 250-bp Illumina HiSeq 2500 platform (Illumina, Inc., San Diego, California). Paired-end sequences were merged by the FLASH tool (Magoc & Salzberg, 2011), then quality-filtered on the QIIME 1 platform (Caporaso et al., 2010). After removing any chimeric sequences using USEARCH (Edgar, Haas, Clemente, Quince, & Knight, 2011), the remaining sequences were assigned to Operational Taxonomic Unit (OTUs) at threshold similarity of 97% by using the UNITE database as a reference (Abarenkov et al., 2010). Taxonomic classification of each representative sequence was assigned with the Ribosomal Database Project's classifier (Cole et al., 2003).

2.5 | Data analysis

All statistical analyses were carried out in the R platform (v3.2.2; http://www.r-project.org/), unless otherwise indicated. Multiple-factor analysis of variance ('MASS' package) and Kruskal–Wallis nonparametric testing ('agricolae' package; De Mendiburu, 2014) were used, respectively, to determine how the explanatory factors affected edaphic variables and to compare significant differences among distinct groups. Principal component analysis was used ('Vegan' package; Oksanen et al., 2007) to investigate the distribution of edaphic variables based on a scaled parameter matrix, fitting these parameters using the envfit function. Boxplots were used to illustrate the distribution of fungal alpha and beta diversity values. Principal coordinate analysis was implemented ('Ape' package), with significant differences in fungal community composition tested by three different but complementary nonparametric multivariate statistical analysis methods (Vegan package): permutational multivariate analysis of variance using distance matrices, analysis of similarities, and multiresponse permutation procedure. Most of the results were visualized by using the 'ggplot2' package (Wickham, 2016). An indicator species analysis ('indicspecies' package) was done (De & Legendre, 2009) and correlations ('Hmisc' package) used to investigate associations between indicator species and edaphic variables. The latter's influence on fungal communities at different temporal stages of succession was studied by a constrained analysis of principal coordinates (CAP) based on Bray-Curtis distances (Vegan package); a forward selection procedure was used and significance confirmed by permutational multivariate analysis of variance before the CAP analysis.

For the network analysis, this was performed for each restoration duration based on strong and significant correlations (both positive and negative) found between abundant fungal genera and all of the edaphic variables (nonparametric Spearman's correlation, $p < 0.01$ with absolute value of $r_s > 0.65$). Before the network analysis, genera with low abundances were eliminated when they constituted <0.005% of the average relative abundance across all samples. Except for the C/N ratio, other edaphic variables were exhibited in the final network. These co-occurrence networks were generated by 'igraph' packages (Csardi & Nepusz, 2006) and visualized by the 'Gephi' interactive platform (Bastian, 2009) using the Yi fan Hu layout. Keystone species (nodes), defined as those who were able to hold communicating nodes together, were identified by betweenness centrality values (Vickmajors, Priscu, & Amaralzettler, 2014). The FunGuild was used to annotate the trophic modes of fungi (Nguyen et al., 2015), using a minimum sequence taxonomy identity >93%, for which a guild confidence ranking of "highly probable" and "probable"was assigned.

3 | RESULTS

3.1 | Variation in soil physico-chemical characteristics

To investigate the distribution of edaphic variables across space and over time, we visualized it using a principal component analysis (Figure 1) combined with three different statistical approaches (**Table S1**). Notable temporal and spatial variations were found in these variables, with R^2-values of 0.456, 0.161, 0.071, and 0.074, for restoration duration, soil layer, slope position, and slope aspect, respectively ($p < 0.001$ for all). Importantly, the variables were clearly separated by restoration duration and soil layer. The within-group differences for restoration duration and soil layer ($\delta = 3.994$ and 4.841, respectively) were lower in magnitude than those for slope position and aspect ($\delta = 5.083$ and 5.087, respectively).

After assessing the variation in edaphic variables between the two soil layers, we found topsoil had significantly higher values than subsoil ($p < 0.05$) for all of them except pH, CEC, $CaCO_3$, and C/N ratio. And the restoration durations were associated with distinct edaphic variables, including a pH and C/N ratio that declined with increasing year. Reversely, soil mineral nutrients, including TN, NH_4^+-N, TP, AP, AK, and CEC, all had higher values with a longer restoration duration. SWC, SOM, and NO_3^--N ranked as 30 years > 5 years > 20 years, whereas $CaCO_3$ showed the inverse trend. Most of these variables showed a significant difference ($p < 0.05$) at 30 years compared with 20 or 5 years of restoration only, whereas SWC, NO_3^--N, AP, and

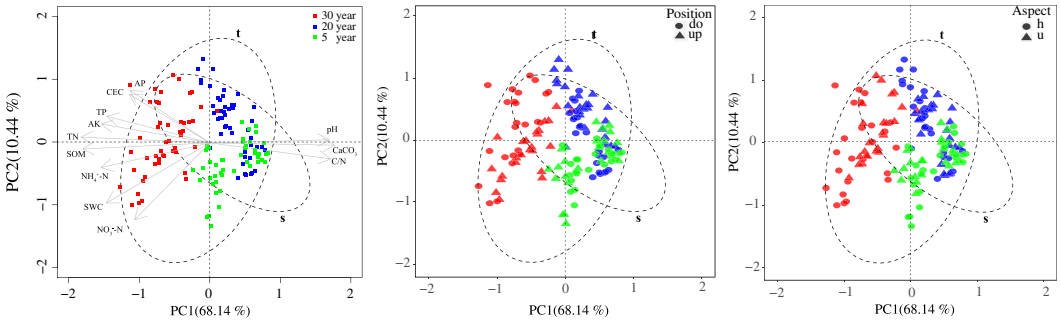

FIGURE 1 Principal component analysis of edaphic variables in the restored grassland on the Loess Plateau. Color of red, blue, and green represents restoration duration; shape of circles represents down and shady slope; shape of triangles represents up and sunny slope; dashed ellipses represent two soil layers based on 95% confidence intervals; and arrows represent edaphic variables in correlation with each other. pH, soil pH; SWC, soil water content; SOM, soil organic matter; TN, soil total nitrogen; NH_4^+-N, soil ammonium nitrogen; NO_3^--N, soil nitrate nitrogen; TP, soil total phosphorus; AP, soil available phosphorus; AK, soil available potassium; CEC, soil cation exchange capacity; $CaCO_3$, Soil calcium carbonate; and C/N, soil total carbon/nitrogen ratio [Colour figure can be viewed at wileyonlinelibrary.com]

AK were significantly different ($p < 0.05$) between all three restoration durations (Table 1).

Next, we investigated differences in edaphic variables between topographic factors in each restoration duration and soil layer (**Table S2**). Generally, the variables did not differ significantly between the two slope positions. Nonetheless, SWC was higher down-slope than up-slope, whereas pH and most other nutrients displayed the reverse pattern. Additionally, soil pH, $CaCO_3$, and C/N ratio were higher on sunny than shaded slopes in both soil layers at 20 and 30 years of restoration. Other variables—SWC, TC, SOM, TN, TP, AP, AK, CEC, NH_4^+-N, and NO_3^--N—were all higher on shaded slopes in both soil layers.

3.2 | Alpha diversity of soil fungal communities

The sequencing run of ITS sequence amplicons yielded a total of 9,867,996 quality reads (after filtering), from the 144 soil samples. Number of sequences per sample ranged from 22,112 to 107,199, with a mean (±standard deviation) of 68,528 ± 10,638 reads. By way of comparison, a total of 5,850,644 reads (59.29% sequences) were classified to the phyla of fungi. A total of 8,783 different OTUs were clustered from the reads, with the number of OTUs per sample varying in the wide range 596–2683 (mean 1224 ± 425).

After homogenization based on 21,558 reads, we inquired further. Generally, fungal taxon numbers at the phylum level were similar in different restoration durations, soil layers, and topography (**Tables S3 and S4**). Interestingly, only one phylum *Neocallimastigomycota* appeared in the up-slope position of topsoil at 20 years of restoration. Other taxonomic levels (from class to genus) showed an increasing trend with temporal succession, always reaching their maximum numbers in the 30-year restoration and topsoil layer.

Across all the samples, the *Basidiomycota* (16.3%), *Ascomycota* (37.4%), *Zygomycota* (5.5%), *Glomeromycota* (0.5%), *Chytridiomycota* (0.01%), and *Neocallimastigomycota* (0.0001%) represented all the annotated phyla. The mean relative abundances of these dominant lineages showed distinct temporal and spatial distributions. All these phyla were more abundant in topsoil, whereas the uncommented phyla ("others") were higher in subsoil. Over time, both *Basidiomycota* and *Chytridiomycota* decreased in relative abundance from 5 to 30 years of restoration, whereas the other phyla increased with temporal succession (except for *Neocallimastigomycota*). Furthermore, the fungal phyla in soil were slightly distinguishable in their abundance between topographic factors (**Figure S2**).

The four-factor multivariate analysis of variance showed that different factors had varying effects on the alpha diversity indices of soil fungal communities (**Table S5**). Restoration duration and soil layer had the most pronounced and significant effects ($p < 0.001$; respective F-values of 164.77 and 43.37, 183.34 and 56.87, and 172.82 and 56.47, for the Shannon, ACE, and Chao1 indices), whereas slope position and aspect negligibly affected alpha diversity. Considered in more detail, the alpha-diversity index values consistently increased with a longer restoration duration, being significantly different at 30 and 20 years compared with 5 years of restoration. These indices followed a similar trend of higher values in topsoil as restoration progressed (Figure 2a,d,g). In both soil layers, there were slightly higher values in down-slope positions at 30 years, yet higher values were found up-slope at 20 and 5 years of restoration (except for the reverse trend in topsoil at 5 years; Figure 2b,e,h). Apart from the Shannon index for 5-year–restored subsoil, these alpha-diversity indices were also higher on the shaded slope in both soil layers after 20 and 5 years of restoration (Figure 2c,f,i). In sum, fungal alpha-diversity possessed temporal and spatial distinction during grassland restoration on this site of the Loess Plateau.

3.3 | Beta diversity of soil fungal communities

The principal coordinate analysis revealed that the constrained PCo1 axis explained 21.80% of the total variance, whereas the constrained PCo2 axis explained 13.76% of the total variance in fungal community

TABLE 1 Differences in edaphic variables among restoration durations (n = 48) and soil layers (n = 72)

		pH	SWC (%)	SOM (g·kg-1)	TN (g·kg-1)	NH_4^+-N (mg·kg-1)	NO_3^--N (mg·kg-1)	TP (g·kg-1)	AP (mg·kg-1)	AK (mg·kg-1)	CEC (cmol·kg-1)	$CaCO_3$ (g·kg-1)	C/N
Restoration duration (years)	30	8.1 ± 0.09 a	13.47 ± 3.44 a	42.85 ± 6.12 a	2.75 ± 0.46 a	103.87 ± 59.84 a	155.52 ± 66.66 a	0.95 ± 0.11 a	7.03 ± 1.52 a	157.97 ± 57.24 a	13.06 ± 3.52 a	0.93 ± 0.23 a	12.31 ± 1.65 a
	20	8.36 ± 0.1 b	5.75 ± 1.7 b	19.53 ± 5.53 b	1.44 ± 0.35 b	17.95 ± 13.02 b	90.86 ± 34.01 b	0.8 ± 0.06 b	5.46 ± 1.99b	103.7 ± 42.87 b	8.84 ± 4.65 b	1.72 ± 0.15 b	22.23 ± 5.17 b
	5	8.39 ± 0.15 b	9.57 ± 2.43 c	21.45 ± 6.79 b	1.34 ± 0.36 b	17.19 ± 14.9 b	119.29 ± 68.24 c	0.79 ± 0.05 b	3.41 ± 1.91 c	84.11 ± 32.69 c	7.12 ± 0.47 b	1.69 ± 0.17 b	23.7 ± 5.57 b
Soil layer	Topsoil	8.2 ± 0.14 a	10.94 ± 4.99 a	32.71 ± 11.1 a	2.12 ± 0.68 a	64.95 ± 63.74 a	144.33 ± 71.76 a	0.87 ± 0.11 a	5.98 ± 2.22 a	147.66 ± 45.55 a	9.61 ± 3.33 a	1.34 ± 0.37 a	16.51 ± 3.73 a
	Subsoil	8.36 ± 0.17 b	8.25 ± 2.28 b	23.17 ± 11.52 b	1.56 ± 0.72 b	27.72 ± 34.96 b	99.45 ± 45.16 b	0.83 ± 0.11 b	4.61 ± 2.28 b	82.87 ± 43.23 b	9.74 ± 4.92 b	1.55 ± 0.42 b	22.32 ± 7.8 b

Note. pH: soil pH; SWC: soil water content; SOM: soil organic matter; TN: soil total nitrogen; NH_4^+-N: soil ammonium nitrogen; NO_3^--N: soil nitrate nitrogen; TP: soil total phosphorus; AP: soil available phosphorus; AK: soil available potassium; CEC: soil cation exchange capacity; $CaCO_3$: soil calcium carbonate; C/N: soil total carbon/nitrogen ratio. Values are mean ± standard deviation. Values within the same column followed by different letters are significantly different (p < 0.05).

composition (based on Bray–Curtis dissimilarity distances). Fungal community composition was clearly separated by soil layer and restoration duration, though with lower distinction between soil layers over temporal succession (Figure 3); this pattern was verified by multiple statistical approaches (Table 2). There were significant differences (p = 0.001) in fungal community composition between soil layers, 30 years (R^2 = 0.085, R = 0.200, δ = 0.526) < 20 years (R^2 = 0.260, R = 0.728, δ = 0.579) < 5 years (R^2 = 0.311, R = 0.861, δ = 0.606). Correlation of fungal community clusters between soil layers was strongest at 30 years (r = 0.37, p = 0.001; Table 3), corroborating the compositional similarity (i.e., 30 > 20 > 5 years) found above based on the Bray–Curtis distance matrix of the same data.

Furthermore, we observed distinct differences in fungal community composition between topographic factors (**Figure S3A**), but these were not as well separated as found for soil layer and restoration duration according to multiple statistical approaches (**Table S6**). We then investigated the distributions of fungal communities between topographic factors in each soil layer per restoration duration (**Figure S3B**), finding significant differences in both soil layers at 30 years. The same trend was seen for 20 years of restoration, but these differences were less significant for aspect than position, and likewise for 5 years of restoration. In sum, fungal community variation between topographic factors was most pronounced after a longer duration of grassland restoration.

3.4 | Co-occurrence and dynamics of soil fungal communities

We then investigated interactions between edaphic variables and fungal communities in different restoration durations through co-occurrence networks, because community structure clearly had changed through succession. The network structure was distinct (Figure 4), featuring similar nodes but different edges: the 20-year restoration network had four times as many edges (**Table S7**) as found in other two restoration networks. Compared with the other restoration networks, the 30-year restoration network had distinct topological features in showing evidence of modular feature partitioning (modularity index was 0.721 > 0.4; values >0.4 suggest that the network has a modular structure).

Building on this, we assessed indicator species at the genus level (**Table S8**), annotating them in the networks with red-colored node names; similarly, we annotated keystone nodes (**Table S9**), representing the first six highest values of betweenness centrality in every network, with green-coloured names. Comparing the networks, keystone species assembled toward the middle of networks but indicator species were scattered around networks through temporal succession, with significant relationships to edaphic variables. Interestingly, in terms of edaphic variables and fungal genus associations, keystone nodes of edaphic variables (green node names) in the restoration networks were consistent with the significant environmental factors derived from the CAP (**Table S10**).

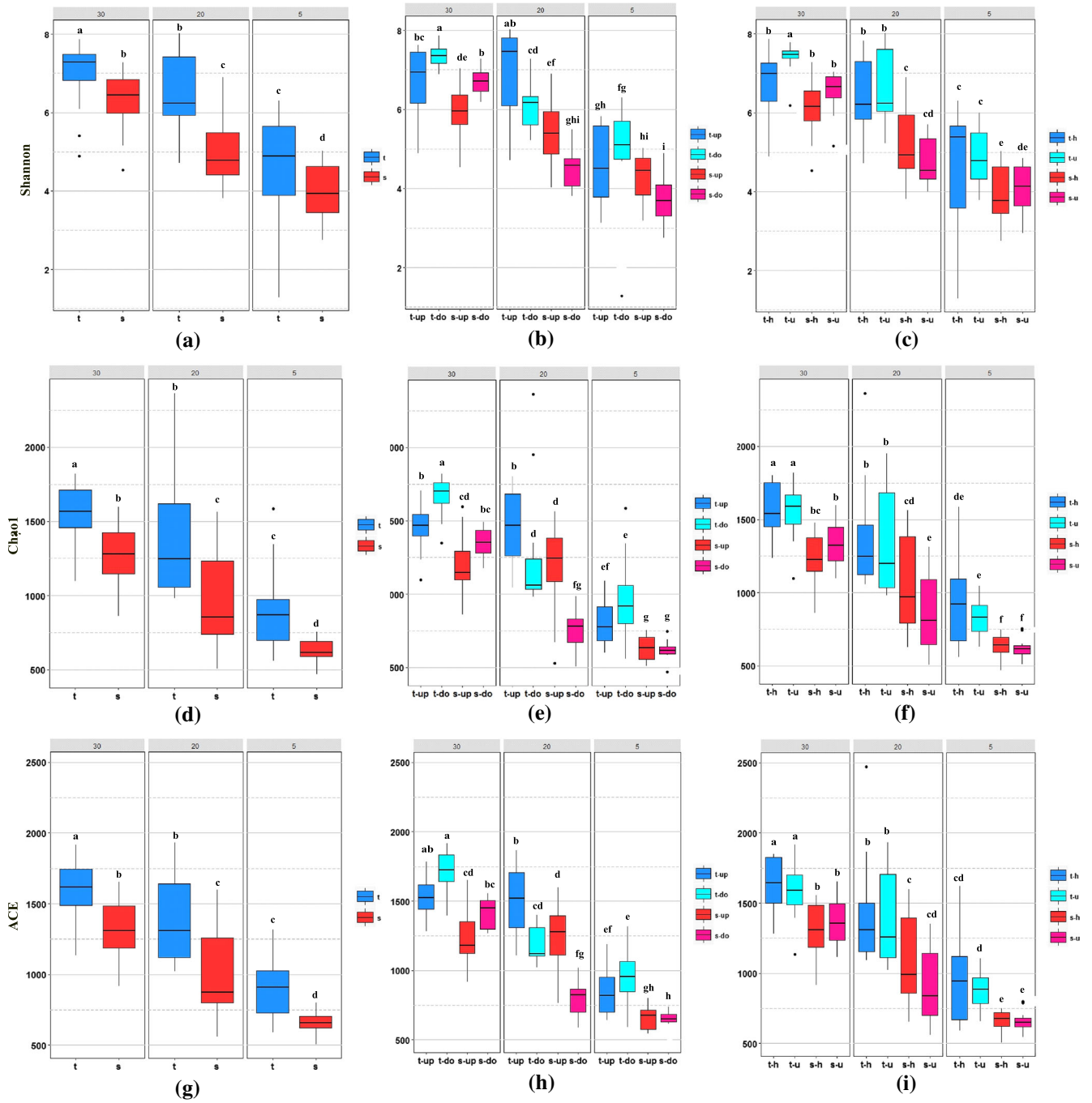

FIGURE 2 Boxplot of the alpha-diversity indices of soil fungi in the restored grassland. (a–c) Shannon; (d–f) Chao1; and (g–i) ACE. The index values at each restoration duration (5, 20, and 30 years) are averaged by soil layer (topsoil and subsoil; a, d, and g), slope positions (up- and down-slope; b, e, and h), and slope aspect (sunny- and shaded-slope; c, f, and i). Different letters are significantly different ($p < 0.05$) [Colour figure can be viewed at wileyonlinelibrary.com]

Most indicator species belonged to *Ascomycota* and *Basidiomycota* phyla, except for *Zygomycota* only occurring at 20 years of restoration. Based on their relative abundances, we categorized the general indicator species into three groups corresponding to restoration duration and examined their association with edaphic variables. Genera assemblages differentially responded to changes in soil variables (Table 4). Significant correlations were nearly apparent at 30 years of restoration. For example, pH had a negative correlation with indicator genera groups, whereas positive correlations were found with SWC, SOM, TN, and NH_4^+, given their autocorrelation. Interestingly, correlations with some variables changed depending on the restoration duration. For example, at 5 years, NH_4^+ and AK had negative relationships with indicator genera groups; at 20 years, there was a negative correlation with SWC;

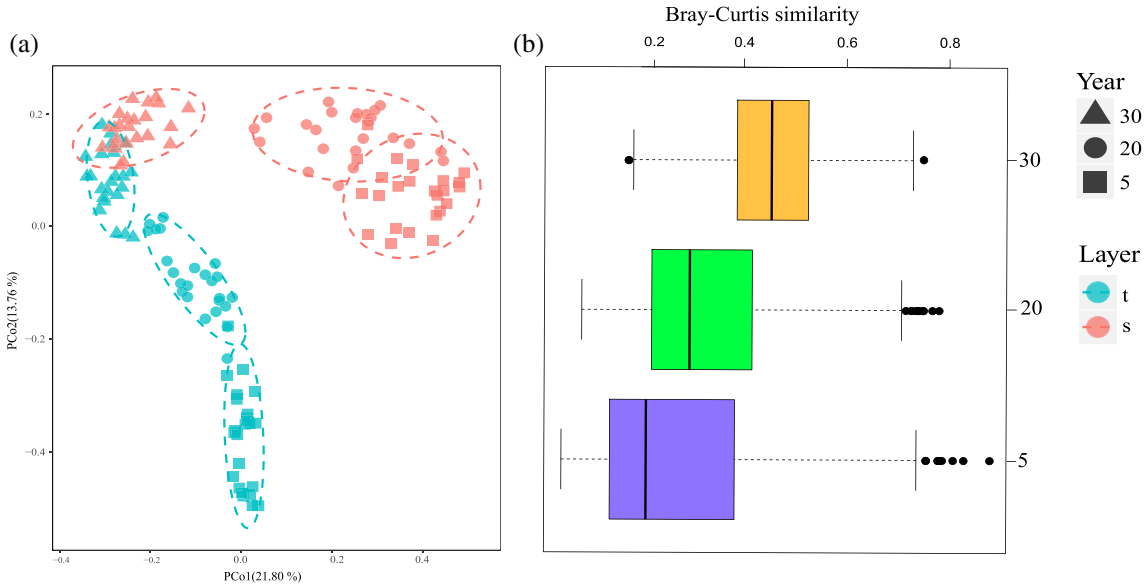

FIGURE 3 Principal coordinate analysis of soil fungal community composition in the restored grassland based on Bray–Curtis distances. (a) Community composition in different restoration durations and soil layers; (b) Boxplot of fungal community similarity. 5, 20, and 30 represent 5, 20, and 30 years of restoration; and t and s represent topsoil and subsoil, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Effects of soil layer on fungal community composition divided by restoration duration with different statistical approaches

	ADONIS		ANOSIM		MRPP	
Dataset	R^2	*p*	R	*p*	δ	*p*
30 years	0.085	**0.001**	0.200	**0.001**	0.526	**0.001**
20 years	0.260	**0.001**	0.728	**0.001**	0.579	**0.001**
5 years	0.311	**0.001**	0.861	**0.001**	0.606	**0.001**

Note. ADONIS: analysis of variance using distance matrices; ANOSIM: analysis of similarities; MRPP: multiresponse permutation procedure. Significant analysis based on 999 times permutation test; bold *p* values indicate significant difference ($p < 0.05$).

TABLE 3 Mantel tests for correlations between fungal community composition in topsoil versus subsoil for each restoration duration based on Spearman's coefficient

Correlation	*r*	*p*
30-year restored topsoil vs. subsoil	0.37	**0.001**
20-year restored topsoil vs. subsoil	0.07	0.275
5-year restored topsoil vs. subsoil	−0.06	0.703

Note. Significant analysis based on 999 times permutation test; bold *p* values indicate significant difference ($p < 0.05$).

and at 30 years, positive and negative relationships were found with NO_3^- and CEC, respectively.

As temporal succession proceeded, the correlations with edaphic variables changed with the dynamics of indicator genera. For instance, absolute correlation coefficients of pH, SOM, TN, and $CaCO_3$ increased over time, whereas those of TP and AP were greatest at 5 and 20 years of restoration, respectively. These above patterns were confirmed in the built co-occurrence networks and their detailed edge coloring, wherein, TN and SWC had significantly positive and negative relationships with general indicator species at 30 and 20 years of restoration, respectively. Because of nonsignificant correlations at 5 years of restoration, the indicator genus *Rutstroemia* lacked direct relationships with corresponding soil variables manifested in the fungal community network.

3.5 | Variation in fungal trophic guilds

Of all sequences, 20.5% of them could be assigned into seven fungal trophic guilds that showed evidence of temporal and spatial variability. For example, these guilds were more abundant in topsoil than subsoil, and except the symbiotroph and saprotroph–symbiotroph guilds, relative abundances of all guilds increased with temporal succession. Different slope positions and aspects favored some fungal guilds over others; for example, both symbiotroph and saprotroph–symbiotroph were more common up-slope and on the shaded slope in topsoil at 5 years of restoration (**Figure S4**).

According to the distribution of fungal trophic guilds (**Figure S5**), both soil layers and three restoration durations were largely separated, yet topographic factors did not divide well. The slope aspect had no significant effects on trophic guild composition (**Table S11**), unlike its

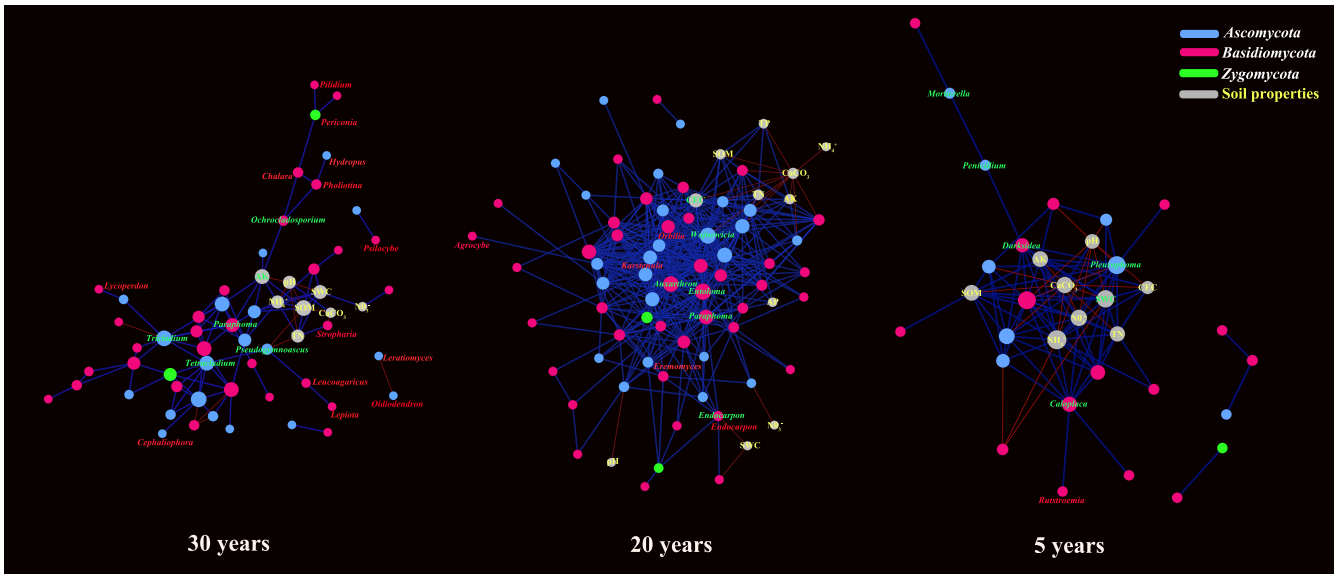

FIGURE 4 Co-occurrence networks of soil fungal communities in the grassland restored for different restoration durations. Color of nodes, fungal phylum; green node name, keystone nodes; red node name, indicator species; yellow node name, edaphic variables; blue edges, positive correlation; and red edges, negative correlation [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Correlations between edaphic variables and average relative abundances of fungal general indicator species grouped by restoration duration

Groups	pH		SWC		SOM		TN		NH_4^+		NO_3^-	
Correlation	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
30 years	**−0.484**	**0.015**	**0.585**	**0.033**	**0.575**	**0.004**	**0.454**	**0.016**	**0.623**	**0.016**	0.292	0.196
20 years	−0.157	0.236	**−0.263**	**0.021**	0.234	0.319	0.341	0.115	0.014	0.678	−0.306	0.163
5 years	−0.096	0.644	0.098	0.501	0.056	0.993	0.052	0.927	−0.176	0.210	−0.068	0.254
	TP		AP		AK		CEC		$CaCO_3$		C/N	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
30 years	0.013	0.733	0.097	0.980	0.463	0.080	−0.075	0.302	−0.252	0.199	−0.227	0.151
20 years	0.242	0.181	**0.483**	**0.009**	0.222	0.156	0.556	0.293	−0.238	0.338	−0.326	0.111
5 years	0.295	0.964	0.179	0.390	−0.051	0.415	0.121	0.716	−0.009	0.380	−0.045	0.993

Note. pH: soil pH; SWC: soil water content; SOM: soil organic matter; TN: soil total nitrogen; NH4+: soil ammonium; N03−: soil nitrate; TP: soil total phosphorus; AP: soil available phosphorus; AK: soil available potassium; CEC: soil cation exchange capacity; CaCO3: soil calcium carbonate; C/N: soil total carbon/nitrogen ratio. *r* represents correlation coefficient, *p* represents significance of correlation, and bold values represent significant difference ($p < 0.05$).

effect on fungal community composition (Table 2). Interestingly, with temporal succession, fungal trophic guilds could be better distinguished between soil layers, in contrast to regular distributions that characterized the composition of fungal communities during grassland restoration.

4 | DISCUSSION

4.1 | Temporal and spatial variation of soil quality

In this study, edaphic variables showed considerable temporal variation in the natural restored grassland on the Loess Plateau. This could be attributed, in part, to different restoration durations, which suggests that habitat specificity exist for plants and soil microbiota (Wang et al., 2017). When considered alongside the spatial variation, we found within each restored grassland habitat, it is perhaps not surprising temporal variation in edaphic variables was stronger. Generally, soil nutrient conditions improved and tended to stabilize at our study site with a longer restoration duration, a view supported by previous studies on the Loess Plateau (Liu et al., 2017; Zhang, 2017). For example, SOM and SWC had increasing trend from 5 to 30 restoration durations, and that TN, NH_4^+-N, AP, and AK all had higher values with a longer restoration duration, which all elucidated the improved soil quality. Our results showed that soil water and nutrient contents were

generally the greatest in topsoil, which mostly agrees with previous studies (Jiao et al., 2018; Sagova-Mareckova et al., 2016). Reversely, lower pH, C/N ratio, CEC, and $CaCO_3$ occurred in topsoil due to various factors. The root length of grassland plants is short and always distributed around the topsoil. This would point to more acid root exudates and nutrient exchange occurring in topsoil, so that soil pH and C/N ratio were lower than in subsoil.

We found that edaphic variables were inconsistent across slope positions and aspects. These topographic patterns could be attributable to the degree of soil erosion associated with water or nutrient transport (Gabarrón-Galeote, Martínez-Murillo, Quesada, & Ruiz-Sinoga, 2013; Owono, Ntamak-Nida, Dauteuil, Guillocheau, & Njom, 2016) and soil temperature with respect to solar radiation (Kang, 2001). SWC was higher down-slope and on shaded slopes because of various accumulation and evaporation forces shaped by distinctive microtopography. In addition, most soil nutrients attained higher concentrations up-slope and in shaded conditions. A study recently reported that upward slopes featured stable soil conditions (Conforti, Lucà, Scarciglia, Matteucci, & Buttafuoco, 2016), which may be one reason for the nutrient distributions found in our study. Soil pH, $CaCO_3$, and C/N ratio were increased on sunny slopes, which could not be explained solely by their negative relationships with SWC. Under lower water conditions, $CaCO_3$ probably accumulated because of lower solubility, whereas higher C/N ratio was may be attributed to nutrients differentiated distribution (Brockett, Prescott, & Grayston, 2012). Moreover, a lower water content would have increased soil salinity, leading to a soil pH veering toward alkalization (Hall, Cammeraat, Keesstra, & Zorn, 2016).

4.2 | Temporal and spatial succession of fungal communities

With temporal succession, taxon numbers at different levels showed a similar trend of increase because of improved soil quality through restoration time. Most soil fungi are aggregated in soil with suitable conditions, so their distributions or relative abundances are expected to have intimate relationships with surrounding local soil properties. For example, the phylum *Neocallimastigomycota* only appeared in the up-slope position of topsoil in the grassland restored for 20 years. Members of the *Neocallimastigomycota* have been reported to be anaerobic fungi (Joshi et al., 2018) and they are known to depolymerize complex molecular structures, which is useful for degrading lignocellulose biomass (Da, Pedezzi, & Souto, 2017). The latter suggests this phylum could degrade lignocellulose at our study site without anaerobic conditions, which may be attributed to their different living environment. All fungal phyla we detected in our samples had higher relative abundances in topsoil, and became more abundant as temporal succession proceeded, but *Basidiomycota* and *Chytridiomycota* decreased from 5 to 30 years. This exception could be explained both phyla preferred to oligotrophic environments (James et al., 2006; Wijayawardene et al., 2018) and this situation existed in initial restoration durations from our study.

The alpha diversity (community structure) of soil fungi in the restored grassland was strongly influenced by restoration duration and soil layer because of relatively large corresponding differences in edaphic variables. However, the effects of topography on soil fungi were limited to alpha diversity. Generally, alpha diversity changed much like the relative abundance of fungal phyla, being variously distributed according to topographic factors among restoration durations and between soil layers. Our results on the Loess Plateau are in agreement with some studies that suggested the alpha diversity of soil fungi is improved along successional pathways of afforestation and natural grasslands (Dang et al., 2017; Zhang, 2017). In our study, fungal alpha diversity was always greater in topsoil, because this soil layer had more soil nutrients that better accommodated eutrophic fungal communities to live in. In particular, the distribution of plant roots and their excretions in the topsoil layer could enrich many eutrophic fungal communities (Fan et al., 2017).

Our results showed that spatial distribution patterns of soil fungal communities changed with temporal succession of grassland on the Loess Plateau. The smallest differences of fungal community composition between soil layers were observed at 30 years, compared with those at 20 and 5 years of restoration. This reflects the temporal and spatial cosuccession of soil fungal communities occurring in the restored grassland. As restoration proceeds, soil is developed into a more stable condition, thus reducing the disparity of soil nutrients between soil layers. Another consideration is the growth of vegetation during restoration, including plant species and their root lengths. Some studies that surveyed aboveground plants reported them as having considerable effects upon edaphic variables and soil microorganisms (Guo et al., 2018; Xiao, Fan, Wang, Chen, & Wei, 2017; Yang, Dou, Huang, & An, 2017). In addition, we found significant topography-driven differences in soil fungal communities, despite being smaller than those linked to restoration duration and soil layer. Similarly, a few studies have reported that soil microbial communities and arbuscular mycorrhizal fungal communities could be considerably affected by soil exposure under different topographic conditions in alpine ecosystems (Bardelli et al., 2017; Chai et al., 2018).

Importantly, at a small scale, the soil fungal communities always manifested a different composition in a special niche with different topographic factors, and we found a divergent spatial (topography) succession of fungal communities through restoration time, not unlike their spatial vertical distinction through soil layers. In sum, spatial succession patterns of fungal communities with soil layer and topography concurrently changed during temporal succession in the restored grassland habitats.

4.3 | Co-occurrence network and dynamics of fungal communities

Soil fungal communities may be correlated not only with soil nutrients but also among themselves through various mechanisms (Ma et al., 2016). In our co-occurrence networks, that of the 30-year restoration

had unique topological features and signs of modular partitioning by fungi, which was attributed to soil development under secondary succession of grassland. However, the interactions of edaphic variables and fungal communities were more complicated in the 20-year restoration network rich in edges. This result may be related to SWC and SOM being the lowest and SWC being negatively correlated with the indicator groups of soil fungi for the restoration duration (i.e., 20 years).

Recently, a study reported that networks of soil bacterial communities were more complicated under higher precipitation regimes (Wang, Wang, Han, & Deng, 2018), because an increasing biomass stimulated by a greater supply of water and nutrients provides more opportunities for different species to interact with each other. By contrast, in our study, soil fungal communities formed complex networks under the stress of water and organic matter. In contrast to soil bacteria, soil fungal spores could remain dormant and they could existed long time before metabolic potential was stimulated under appropriate condition (Creamer et al., 2016). Moreover, a low SWC may not only stress fungal communities but also affect the dissolution and fluidity of soil nutrients, in addition to low SOM, forcing fungal communities to enhance their interspecific communication and nutrient transport to sustain life in the form of complex co-occurrence networks at 20 years of restoration.

The distribution patterns of indicator and keystone species of soil fungi changed through grassland restoration, yet keystone species assembled toward the center of the network with temporal succession, that was due to keystone species always had more stable effects on the whole structure of fungal communities (Banerjee, Schlaeppi, & van der Heijden, 2018). We found that keystone species of soil fungi may be less affected by external environmental factors, over a relatively short time, and this points to their more solid role in the dynamics of fungal communities, underpinning the more stable soil conditions. Keystone nodes of edaphic variables were the very same significant edaphic variables from the CAP results, which demonstrate the accuracy of our established networks as well as the regulation of fungal communities by edaphic variables in this restored grassland habitat. Moreover, fungal indicator genera were scattered more around the 30-year restoration network suggesting they were more sensitive to variation in edaphic variables after 30 years of succession. In the beginning of secondary succession of grassland, edaphic variables changed fast and the response of indicator species may have lagged behind. Further, our indicator assemblages showed various nonrandom associations with edaphic variables, especially at 30 years, when more significant correlations existed. However, in the early stage of restoration (5 years), such correlations were not found. Therefore, we could assess the state of soil restoration in grassland via these indicator species and their predicted correlations with edaphic variables; this would be similar to using species to gauge mine drainage impacts on surrounding soil environments (Fan et al., 2016). In addition, we could try to isolate these indicator or keystone species to construct beneficial assembly communities and inoculate them into degraded soil to hasten grassland restoration (Wubs, van der Putten, Bosch, & Bezemer, 2016).

Fungal trophic guilds have habitat-specific adaptations, and pathotroph and saprotroph guilds are more inclined to nutrient-enriched environments (Nguyen et al., 2015; Zhang, Adams, et al., 2017), such as topsoil with its higher oxygen and humus content. With temporal succession, more soil nutrients and plant litter material become available for fungal trophic digestion, especially for the pathotroph guild whose hosts are well-represented by plants and soil microorganisms. Here, we found that symbiotroph and saprotroph-symbiotroph guilds had higher relative abundances at 5 years of restoration, for which the locust (*Robinia pseudoacacia*) was also abundant because of slight artificial plantation. In addition, some symbiotroph fungi could have become saprotrophic due to improved nutrient availability instead of exchanging resources with host cells. In our study, the relative abundance of *Basidiomycota* was higher at 5 years of restoration, and most symbiotic mycorrhizal fungi derive from this phylum (Shah et al., 2016). Classes of *Sordariomycetes* and *Agaricomycetes* are regarded as saprotrophic taxa (Zhang, Adams, et al., 2017), but in our grassland, the *Agaricomycetes* abundance declined with temporal succession, which was inconsistent with the variation in fungal trophic guilds. This discrepancy could be explained by the different types of soil and vegetation in the present study compared with other studies to date.

These trophic guilds share similar metabolic characteristics of keystone species, because most keystone species we found belonged to the *Ascomycota* phylum, which feed on a variety of organic substrates including dead matter and foodstuffs. Owing to their long evolutionary history, the *Ascomycota* have evolved the capacity to break down almost every organic substance it comes into contact with, and they can use their own enzymes to digest complex plant biopolymers such as cellulose or lignin (Lutzoni et al., 2004). Finally, the functional features of soil fungi had distribution unlike that of fungal communities; in particular, their spatial succession patterns were completely opposite. That was similar with the study reported that warming significantly affected the functional structures of microbial communities, but taxonomic structures were not clearly seperated (Cheng et al., 2017). Because functional characteristics were closely related to the changes in the functional gene structure of microbial communities.

5 | CONCLUSION

In this study, we investigated temporal and spatial variation in edaphic variables and linked these to the succession and dynamics of soil fungal communities in restored grassland on the Loess Plateau. Edaphic variables showed considerable differences with restoration duration and soil layers but varied much less with topography. The patterns of fungal alpha and beta diversities changed dynamically with temporal succession, in particular, with respect to the spatial succession of fungal community composition. Co-occurrence networks of edaphic variables and fungal communities had distinct structures and distribution patterns of indicator and keystone species for each restoration duration of 5, 20, and 30 years. The functional adaptation of fungal communities corresponded well to the soil habitats

generated by succession underpinning the grassland restoration process. Future work should consider isolating indicator or keystone species of soil fungi from the standpoint of culture-omics based on our findings and then aim artificially restructure fungal communities in practice to restore stable soil conditions within degraded lands at a small spatial scale.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

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